PASPALUM VAGINATUM (POACEAE), A NEW THREAT TO WETLAND DIVERSITY IN SOUTHERN CALIFORNIA

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ABSTRACT

Paspalum vaginatum, a warm-season perennial grass known from tropical and subtropical regions around the world, is reported for the first time for California. We review its distribution, ecology, anthropogenic uses, invasive status, and biological traits promoting its invasive behavior worldwide and in southern California, where it likely arrived as a purposeful human introduction in the 1970s and 1980s. Anthropogenic disturbances, its widespread use in the turf industry, and broad ecological tolerances help to explain its explosive spread and rapid establishment. *Paspalum vaginatum* is now widespread and often highly invasive in estuarine wetlands in southern California. Our preliminary observations, and anecdotal evidence and quantitative data gathered in other countries suggest its impacts to native ecosystems are similar to those of the better-documented nonnative cord grasses (*Spartina* spp.). Accordingly, the long-term consequences of *P. vaginatum* invasions could pose a serious threat to native biodiversity and ecosystem function of estuarine wetlands in southern California. Likely unrecognized in the field for decades, the presence of *P. vaginatum* indicates that focused floristic and taxonomic studies are urgently needed to thoroughly document the nonnative flora of wetland communities throughout urbanized southern California.

Key Words: biodiversity, ecosystem transformers, estuarine wetlands, invasive plants, mudflats, *Paspalum vaginatum*, salt marsh, seashore paspalum, wildland-urban interface

RESUMEN

Paspalum vaginatum, una hierba perenne de clima cálido procedente de las regiones tropicales y subtropicales del mundo, se cita por primera vez en California. Revisamos su distribución, ecología, usos antropogénicos, estatus invasivo y los rasgos biológicos que promueven su comportamiento invasivo en el mundo y en el sur de California, donde probablemente llegó debido a la introducción humana deliberada en las décadas de los 1970 y 1980. Las alteraciones antropogénicas, su uso generalizado en la industria del césped y su amplia tolerancia ecológica permiten explicar su propagación explosiva y su rápido establecimiento. *Paspalum vaginatum* está actualmente ampliamente propagada, y con frecuencia con carácter altamente invasivo, en los humedales de los estuarios del sur de California. Nuestras observaciones preliminares, así como la evidencia anecdótica y los datos cuantitativos acumulados en otros países, indican que su impacto en ecosistemas nativos o autóctonos es similar a aquel de los mejor documentados pastos cordón no nativos (*Spartina* spp.). Por lo tanto, las consecuencias a largo plazo de las invasiones de *P. vaginatum* podrían plantear serias amenazas a la biodiversidad nativa y a las funciones del ecosistema de los humedales de los estuarios del sur de California. La presencia de *P. vaginatum*, probablemente no reconocida en el campo por décadas, indica que urgentemente se necesitan llevar a cabo estudios de floricultura y taxonomía orientados para documentar minuciosamente la flora no nativa de las comunidades de humedales a lo largo de las zonas urbanas del sur de California.

INTRODUCTION

Plant invasions are a major issue for ecosystems around the world (Williamson 1996; Gurevitch & Padilla 2004). The globalization of trade, rapidly expanding urbanization, intensive agriculture and horticultural practices, increasing degradation and fragmentation of natural habitats, biogeographical factors, and climate change are some of the driving forces that increase the movement of species around the world (Mooney & Hobbs 2000; Vila & Pujadas 2001; Myers & Bazely 2003; Pyšek & Richardson 2006). As a result, the flora in many regions of the United States, including California, is now rich in nonnative (alien, exotic) plants (Westbrooks 1998; Bossard & Randall 2007).

Invasive plant species reproduce in very large numbers, are superior competitors, and have the potential to spread across large areas and at considerable distances from parent plants (Richardson et al. 2000). Environmental plant pests (species that affect the loss of native biodiversity) and ecosystem transformers

(species that alter the character, condition, form, or function of ecosystems) pose a serious threat to wildlands in California and elsewhere (Randall 1997; Vitousek et al. 1997; Richardson et al. 2000; Bossard & Randall 2007). In California's estuarine wetlands, some of the most problematic and well-known ecosystem transformers are the introduced *Spartina* species, especially *S. alterniflora* Loisel. and its hybrids (Callaway 2005; California Conservancy 2007).

Historically, the coastal plains of California have been exposed to multiple introductions for long periods of time, and consequently they support more nonnative plant species than many other parts of the state (Randall et al. 1998; Bossard & Randall 2007). Wetlands are especially vulnerable to plant invasions, particularly in coastal or urban areas that experience significant pressures from human activities (Galatowitsch et al. 1999; Ruiz et al. 2000; Callaway & Zedler 2004; Zedler & Kercher 2004). Even salt marshes, which historically have not experienced significant invasions owing to naturally high salinity levels and anaerobic conditions that inhibit establishment of most nonnative plants, are now highly invaded ecosystems (Callaway 2005; Grewell et al. 2007). Accordingly, the proximity of wetlands to large urban centers, which function as landscape sinks, facilitates multiple disturbances, alterations to hydrological regimes, and dissemination of propagules that promote the establishment of nonnative facultative wetland plants (Galatowitsch et al. 1999; Cronk & Fennessy 2001; Zedler & Kercher 2004). In southern California, expanding urbanization provides year-round sources of water from runoff and discharge of wastewaters into natural drainages, which provide direct pathways of dispersal for nonnative species spreading from uplands to wetlands at the wildland-urban interface (White & Greer 2006; Riefner & Boyd 2007).

In this paper, we provide the first documented records of *Paspalum vaginatum* Sw. (Poaceae, Panicoideae, Paniceae) for California. *Paspalum vaginatum* (seashore paspalum, saltwater couch, saltwater paspalum, siltgrass) is widely recognized as a serious invasive pest and an ecosystem transformer that has naturalized in many subtropical and tropical coastal wetland environments, often with detrimental effects to the structure and function of indigenous ecosystems (Graeme & Kendal 2001; Shaw & Allen 2003; Weber 2003; Dana et al. 2004; Siemens 2006). In order to understand the introduction and establishment of this species in southern California, we review its anthropogenic uses and invasive status worldwide, and examine its biological traits that promote invasiveness and the formation of monocultures in estuarine wetlands. Rapidly expanding populations and the formation of dense monocultures pose a serious threat to the structure, function, and biological composition of tidal marshes, sloughs, and mudflats in southern California.

Specimens Seen. The known range of *P. vaginatum* in southern California is depicted on Figure 1. Individual populations documented by voucher specimen data are as follows: **CALIFORNIA. Los Angeles Co.:** City of Malibu, Zuma Lagoon at Westward Beach Rd., UTM (NAD 83) 11S 0331858E 3765305N, elev. 3 m (10 ft), rare, mud flat with *Jaumea*, 4 Nov 2005, *Riefner 05-744* (RSA); City of Malibu, Malibu Lagoon, W lagoon, S of Pacific Coast Hwy., UTM (NAD 83) 11S 0344592E 3767052N, elev. 1 m (3 ft), common on mud flats, channel banks, and in salt marsh with *Frankenia* and *Jaumea*, highly invasive and displacing native species, 8 Jul 2006, *Riefner 06-290* (RSA); City of Malibu, Malibu Lagoon, E lagoon near Surfrider Beach, S of Pacific Coast Hwy., UTM (NAD 83) 11S 0344854E 3767212N, elev. sea level, local but widespread along inlet channel, on mud flats, and in salt marsh with *Salicornia*, 8 Jul 2006, *Riefner 06-293* (RSA); City of Carson, near Victoria Park, Dominguez Channel at Del Amo Blvd., UTM (NAD 83) 11S 0392422E 3746119N, elev. 7 m (23 ft), locally abundant, growing with *Distichlis* and *Atriplex* in saturation zone along channel, 29 Jul 2006, *Riefner 06-327* (RSA); City of Carson, Dominguez Channel, S of Del Amo Blvd. near Carson St., UTM (NAD 83) 11S 0392702E 3745799N, elev. 7 m (23 ft), widespread and well established, growing with and over *Salicornia*, *Distichlis*, and *Atriplex* in saturation zone along channel, 29 Jul 2006, *Riefner 06-330* (RSA). **Orange Co.:** City of San Juan Capistrano, Trabuco Creek, N side of Del Obispo St. at Paseo Adelento St., UTM (NAD 83) 11S 0438127E 3706763N, elev. 27 m (89 ft), uncommon, sandy streambed in shallow fresh water with *Paspalum distichum*, 14 Oct 2003, *Riefner 03-455* (RSA); City of San Juan Capistrano, Trabuco Creek, S side of Del Obispo St. at Paseo Adelento St., UTM (NAD 83) 11S 0438127E 3706763N, elev. 26 m (85 ft), uncommon, sandy streambed in shallow fresh water, 14 Oct 2003, *Riefner 03-456* (RSA); City of Mission Viejo, Oso Creek, ca. 0.5 mi N of Paseo De Colinas on Camino Capistrano, UTM (NAD 83) 11S 0437527E 3714753N, elev. 86 m (281 ft), well established and highly invasive along perennial creek in mud and shallow water discharged from a waste water treatment plant, and in saturated soil in open riparian scrub growing with *Baccharis salicifolia*, *Pulicaria paludsoa*, and *Salix lasiolepis*, 9 Jul 2005, *Riefner 05-543* (RSA); City of Mission Viejo, Oso Creek, ca. 1.4 mi N of Paseo De Colinas on Camino Capistrano, UTM (NAD 83) 11S 0437526E 3715062N, elev. 88 m (282 ft), well established and highly invasive along perennial creek in mud and shallow water discharged from a waste water treatment plant, and in saturated soil in open riparian scrub growing with *Baccharis salicifolia*, *Paspalum distichum*, and *Schoenoplectus americanus*, 9 Jul 2005, *Riefner 05-545* (RSA); City of Laguna Niguel, Aliso Creek, Alica Pwky. at Skate Park Way, UTM (NAD 83) 11S 0433416E 3713654N, elev. 46 m (151 ft), locally established in wet sand in creek with shallow fresh water,

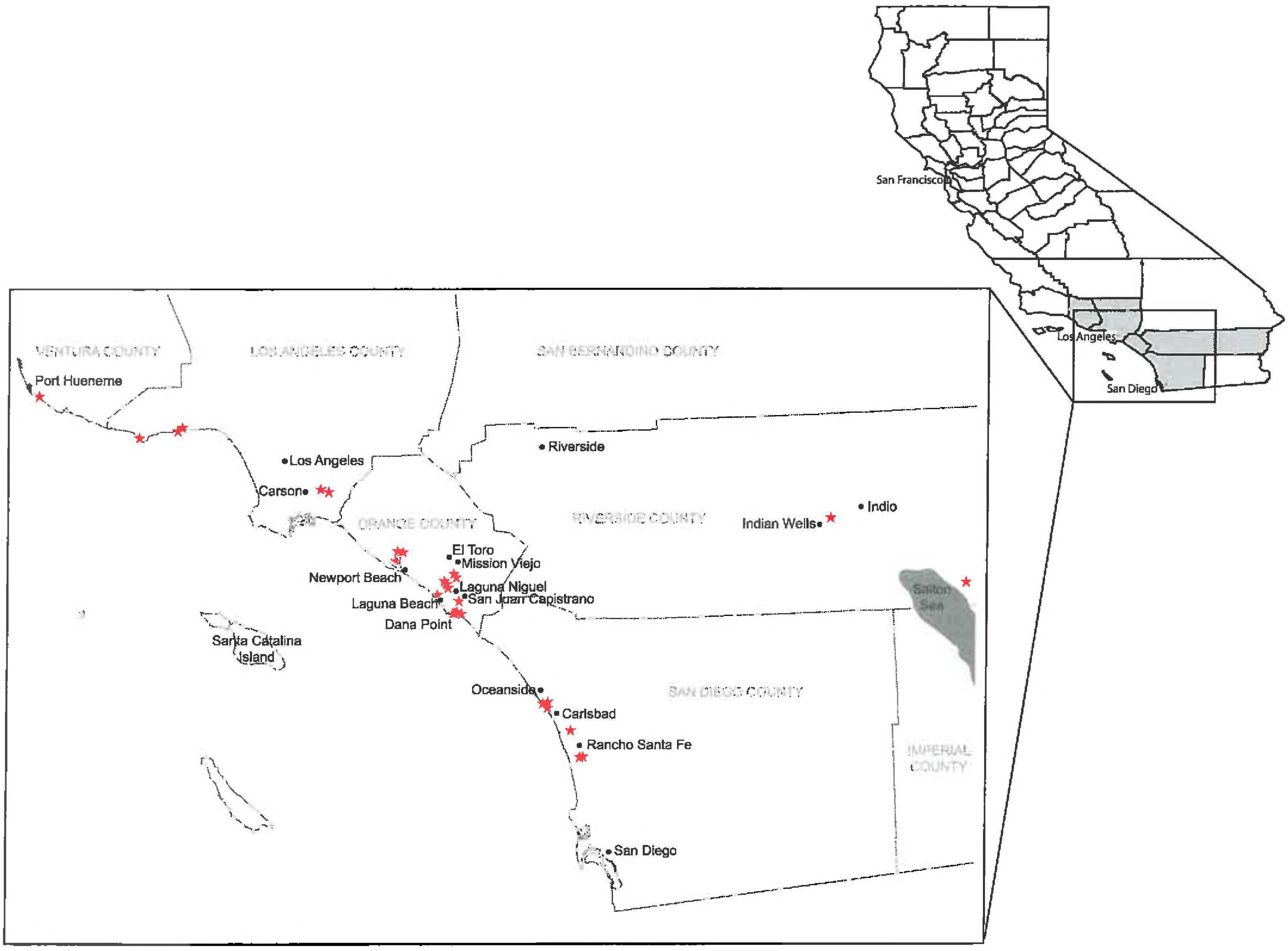

Fig. 1. Known distribution of *Paspalum vaginatum* in southern California. Individual populations documented by voucher specimens (RSA) are shown in red.

growing with *Agrostis*, *Leptochloa*, *Polypogon*, and *Typha*, 8 Jul 2007, *Riefner 07-304* (RSA); City of Newport Beach, E of Jamboree Rd. at Bayview Way, San Diego Creek at confluence with Newport Bay, UTM (NAD 83) 11S 0419719E 3723895N, elev. 6 m (20 ft), tidal wetland, widespread and well established on mud flats and in salt marsh growing with *Salicornia*, *Limonium*, and *Jaumea*, highly invasive and excluding native species, 23 Jul 2007, *Riefner 07-314* (RSA); City of Dana Point, Doheny State Beach, E side of San Juan Creek Lagoon, UTM (NAD 83) 11S 0436583E 3702748N, elev. 4 m (13 ft), locally established but invasive, many individual plants scattered on mud flats and wet sand, 17 Oct 2007, *Riefner 07-434* (RSA); City of Dana Point, Doheny State Beach, W side of San Juan Creek Lagoon, UTM (NAD 83) 11S 0436475E 3702895N, elev. 6 m (20 ft), locally common on dry banks with *Baccharis salicifolia*, and on lagoon mud flats with *Jaumea*, *Aster subulatus* var. *ligulatus*, *Baccharis salicifolia*, *Distichlis*, and *Typha*, 17 Oct 2007, *Riefner 07-436* (RSA); City of Dana Point, Dana Point Harbor, Dana Point Harbor Dr. near Park Lantern Dr., UTM (NAD 83) 11S 0436040E 3702905N, elev. 4 m (13 ft), locally common and invasive, urban creek and adjacent sandy flats with *Cynodon*, *Cyperus involucratus*, *Ehrharta erecta*, *Paspalum dilatatum*, and *Typha*, 17 Oct 2007, *Riefner 07-437* (RSA); City of Dana Point, Doheny State Beach, Dana Point Harbor Dr. near Puerto Pl., UTM (NAD 83) 11S 0435964E 3702721N, elev. 10 m (33 ft), local, sand dune swale with *Distichlis* and *Juncus acutus*, 17 Oct 2007, *Riefner 07-439* (RSA); City of Laguna Niguel, Laguna Niguel Regional Park, vicinity of La Paz Rd. at Aliso Creek, UTM (NAD 83) 11S 0434146E 3712609N, elev. 64 m (210 ft), locally established on creek bank with *Atriplex prostrata* and *Typha*, 26 Oct 2007, *Riefner 07-452* (RSA); City of Laguna Niguel, vicinity of La Paz Rd. at Kings Rd., UTM (NAD 83) 11S 0434619E 3711316N, elev. 64 m (210 ft), locally established in concrete channel draining water-reclamation facility, growing with *Atriplex prostrata* and *Typha*, 26 Oct 2007, *Riefner 07-459* (RSA); City of Newport Beach, North Star Beach, north shore of Newport Bay near North Star Ln., UTM (NAD 83) 11S 0417162E 3721028N, elev. 9 m (30 ft), rare on tidal channel bank and in salt marsh, growing near population of *Cordylanthus mollis* subsp. *maritimus*, 26 Oct 2007, *Riefner 07-461* (RSA); City of Laguna Beach, Aliso Creek at Pacific Coast Hwy., UTM (NAD 83) 11S 0430150E 3708320N, elev. ca. 9 m (30 ft), abundant and invasive on creek banks in tidal waters with *Pulicaria* and *Jaumea*, 13 Jan 2008, *Riefner 08-4* (RSA); City of Newport Beach, San Diego Creek at Hwy. 73, E of Jamboree Rd., UTM (NAD 83) 11S 0419906E 3723854N, elev. ca. 6 m (20 ft), locally established on disturbed creek bank in tidal waters, growing with *Cotula* and *Schoenoplectus*, 13 Jan 2008, *Riefner 08-9* (RSA). **Riverside Co.:** Salton Sink, Dos Palmas Oasis, managed ponds near The Nature Conservancy preserve, 33°30.04'N 115°49.9'W, elev. –37 m (–121 ft), wet soil and shallow water, 4 Dec 1994, *Sanders et al. 15885* (RSA) [originally det. as *Paspalum distichum*; annotated Nov. 2007]; Indian Wells, tributary to Whitewater River, Hwy. 111 near Happy Point, UTM (NAD 83) 11S 0564872E 3730987N, elev. ca. 20 m (66 ft),

uncommon in wet sand along slow-moving waters of urban creek, growing with *Scirpus robustus*, *Leptochloa fusca* subsp. *uninervia*, and *Eclipta*, 7 Aug 2005, *Riefner 05-596* (RSA). **San Diego Co.:** City of Rancho Santa Fe, La Orilla St. at El Camino Real, San Elijo Lagoon, UTM (NAD 83) 11S 477707E 3652459N, elev. 12 m (39 ft), well established on marsh banks and in shallow water with *Ludwigia peploides* subsp. *peploides*, 8 Sep 2002, *Riefner 02-224* (RSA); City of Rancho Santa Fe, La Orilla St. ca. 0.4 mi E of El Camino Real, UTM (NAD 83) 11S 0478231E 3652819N, elev. 21 m (69 ft), well established but local on creek banks and in open marsh, growing with *Aster subulatus* var. *ligulatus*, *Distichlis*, and *Salicornia*, 8 Sep 2002, *Riefner 02-224* (RSA); City of Oceanside, Loma Alta Slough, Buccaneer Park, Pacific St. at Morse St., UTM (NAD 83) 11S 0465660E 3671043N, elev. 1 m (3 ft), well established but local in moist sand and on creek banks, growing with *Distichlis*, *Salicornia*, *Schoenoplectus*, *Jaumea*, and *Atriplex prostrata*, 8 Sep 2002, *Riefner 02-221* (RSA) [originally det. as *Paspalum distichum*; annotated Oct. 2003]; same locality, widespread, highly invasive and excluding native species, 5 Oct 2007, *Riefner 07-420* (RSA); City of Oceanside, Loma Alta Creek at Pacific Coast Hwy., UTM (NAD 83) 11S 0465836E 3671307N, elev. 13 m (43 ft), locally established in creek bed in wet sand near flowing water, growing with *Leptochloa*, *Schoenoplectus californicus*, and *Typha*, 5 Oct 2007, *Riefner 07-420* (RSA); City of Oceanside, Buena Vista Lagoon, Rue des Chateaux at Ocean St., UTM (NAD 83) 11S 0466593E 3669614N, elev. 1 m (3 ft), locally established on mud flat and in disturbed salt marsh, growing with *Jaumea*, *Juncus acutus*, and *Tamarix*, 15 Oct 2007, *Riefner 07-429* (RSA); City of Carlsbad, Batiquitos Lagoon, vicinity of Arenal Rd. at Columbine Dr., UTM (NAD 83) 11S 0474831E 3661679N, elev. 5 m (16 ft), rare, invading *Jaumea* marsh, 15 Oct 2007, *Riefner 07-432* (RSA). **Ventura Co.:** City of Point Hueneme, Bubbling Springs Greenbelt, vicinity of Surfside Dr. and Port Hueneme Dr., UTM (NAD 83) 11S 0297999E 3780473N, elev. 3 m (10 ft), locally common on creek banks, and spreading to shallow water and in marsh with *Ludwigia*, *Typha*, and *Schoenoplectus*, 8 Jul 2006, *Riefner 06-280* (RSA).

PREVIOUS KNOWLEDGE

Distribution.—*Paspalum vaginatum* is a perennial grass documented from warm, coastal regions around the world, including southwest and southeast Europe, tropical Africa, temperate and tropical Asia (Arabia, China, India, Malaysia), Australia, New Zealand, French Polynesia, the Galápagos Islands, Hawaii, and other Pacific Islands, the Caribbean, Central and South America, and the Atlantic and Gulf Coasts of the United States and Mexico in North America (Waterhouse 1997; Allen & Hall 2003; Zuloaga et al. 2003; Clayton et al. 2006). Its exact native range, which is centered in the tropical and subtropical regions of the New World, remains uncertain (Chase 1929; Wagner et al. 1999; Edgar & Connor 2000; Weber 2003). In the United States, *P. vaginatum* occurs from North Carolina to Florida, west in the Gulf States to Texas, and in New Mexico, but was not previously reported for California (Webster 1993; Allen & Hall 2003; DiTomaso & Healy 2007; USDA 2007; Jepson Flora Project 2008).

Across its range, and outside of cultivation, *P. vaginatum* occupies coastal salt and brackish water marshes, shallow-water lagoons and tidal channels, mangroves, coastal shrublands, dunes and beaches, summer-moist saltpans, wet pastures, and freshwater riparian and floodplain habitats in many warm temperate, subtropical, and tropical environments (Skerman & Riveros 1990; Stutzenbaker 1999; Wagner et al. 1999; Edgar & Connor 2000; Filigheddu et al. 2001; Allen & Hall 2003; Shaw & Allen 2003; Dana et al. 2004; Siemens 2006).

Anthropogenic Uses and Worldwide Introductions.—*Paspalum vaginatum* has numerous anthropogenic uses that have transported it to many countries around the world, and eventually to southern California. Historically, it was used as bedding in trade ships that sailed between Africa, North and South America, Central America, and the Caribbean Islands during the 1700s and 1800s (Duncan & Carrow 1999). *Paspalum vaginatum* has also been used widely for rehabilitation of salt-affected lands, stabilization of sand dunes and dredge materials, restoration of coastal wetlands, and forage for livestock (Leithead et al. 1971; OIC 1990; Vargas 1995; NRCS 1999; Loch & Lees 2001; Barrett-Lennard et al. 2003; Fontenot 2007).

As water shortages continue to escalate worldwide, increased use of saline water or poor-quality reclaimed effluent waters for turf landscape irrigation is necessary (Snow 2001). The systematic development and cultivation of varieties (cultivars) of turf grasses with improved tolerance to saline soils and low-quality irrigation waters, including *P. vaginatum*, are playing a central role in the turf grass industry (Henry 1981; Hall 1994; Brown et al. 1998; Carrow & Duncan 1998; Duncan 2003; Marcum 2004). To meet the demands of water conservation and expanding recreational needs, *P. vaginatum* is now grown on golf courses in Asia (including Malaysia, Indonesia, and the Philippines), South Africa, the Middle East, Sardinia, New Zealand, South America, Hawaii, the Caribbean Islands, and across the southern United States (Duncan & Carrow 1999; Beard 2002). *Paspalum vaginatum* is also used as a ground cover in gardens, and new cultivars are

highly promoted for lawns in the southern United States (USDA Zones 7–10), Australia, Hawaii, and elsewhere (Duncan & Carrow 1999; Rushing 2006; Christians et al. 2007; Tukey 2007).

Environmental Tolerances Create a Competitive Advantage.—*Paspalum vaginatum* has broad ecological tolerances and life history traits that aid its widespread establishment and utility to land and resource managers worldwide. It is an ecologically aggressive, rhizomatous and stoloniferous mat-forming perennial grass that often forms extensive colonies (Hitchcock 1951; Weber 2003). It roots well in sand, clay, silt or mucky soils in acidic or alkaline conditions, is tolerant of waterlogged and highly saline soils, prospers in low fertility soils and poor-quality effluent waters used for irrigation, is highly tolerant of mechanical mowing and heavy livestock grazing, has high shoot density for effective soil stabilization, develops a thick low-maintenance turf tolerant of foot traffic and wear, and is not readily susceptible to drought or pathogens (Duncan 1999; Duncan & Carrow 1999; Loch & Lees 2001; Barrett-Lennard et al. 2003; Lee et al. 2004a,b; Fontenot 2007). Therefore, its rapid growth, abundant propagules (in this case rhizome and stolon fragments), and broad environmental tolerances are important characteristics typical of an "ideal weed" (Sakai et al. 2001). In a given environment, these characteristics often confer an advantage to a nonnative species relative to indigenous species (Barney & DiTomaso 2008).

Invasive Status Worldwide.—*Paspalum vaginatum* is well known for its aggressive behavior and its ability to alter wetland ecosystem function (Weber 2003). It is an early and effective colonizer of disturbed, bare or ephemeral soil deposits, and once established it can exclude indigenous species recruitment for many years (Shaw & Allen 2003). *Paspalum vaginatum* is, however, self-incompatible, rarely produces viable seed in significant quantity, and therefore, must be propagated vegetatively (Hall 1994; Duncan & Carrow 1999). However, it would be careless to conclude that species lacking sexual reproduction cannot become serious invaders; giant reed (*Arundo donax* L.) is a classic example of a sterile but highly invasive plant of southern California's riparian habitats (Bossard et al. 2000; Barney & DiTomaso 2008).

Outside of cultivation, vegetative reproduction of *P. vaginatum* would be possible through animal grazing and other natural physical regimes that would disturb and transport rhizomes and stolons (Graeme & Kendal 2001). *Paspalum vaginatum* is apparently dispersed primarily by water when pieces of stolon or rhizome are carried often long distances by streams. These vegetative fragments root easily, forming new plants that start new infestations (Weber 2003). Estuarine mudflats, shallow brackish lagoons or tidal creeks, and gaps in disturbed wetlands or scoured streambeds that are not readily colonized by indigenous species are highly vulnerable to invasion (Filigheddu et al. 2001; Shaw & Allen 2003; Siemens 2006). Importantly, *P. vaginatum* and its impacts on the function of native estuarine ecosystems are significant and comparable to the well-documented invasions by nonnative *Spartina* species (Graeme & Kendal 2001; Allen & Shaw 2003; Dana et al. 2004; Siemens 2006).

In New Zealand estuaries, and much like the ecological impacts effected by introduced *Spartina* species, *P. vaginatum* transforms the composition and structure of indigenous vegetation by growing over and displacing low-stature species, endangering populations of threatened species, altering fish spawning and feeding grounds, prohibiting burrowing fauna and reducing access to feeding sites and roosting by shore birds due to its high shoot and root density, and altering estuarine hydrology by accumulating sediments (Graeme & Kendal 2001; Shaw & Allen 2003).

Similar negative effects in brackish wetlands have been documented in Spain, where *P. vaginatum* displaces halophytes and alters the composition and structure of native communities, promotes accumulation of sediments and organic detritus, and alters hydrological and nutrient regimes (Dana et al. 2004). Accordingly, *P. vaginatum* has been classified as "dangerous" (a species causing ecological damage or alteration to natural ecosystems) (Dana et al. 2007). *Paspalum vaginatum* has also been classified as invasive in Portugal (Domingues de Almeida & Freitas 2006).

In the Galápagos Islands, Ecuador, *P. vaginatum* stands out as a special case. It has aggressively invaded disturbed and natural wetlands where it replaces native plants, and affects water movement and soil moisture content (Vargas 1995; Gravez et al. 2004; Guézou et al. 2007). *Paspalum vaginatum* has also successfully

invaded many lagoons, threatening these ecosystems and their globally significant avifaunal biodiversity. Quantitative investigations have determined that *P. vaginatum* infestations are responsible for degrading fiddler crab habitat, and for altering foraging habitat of aquatic birds by decreasing surface water availability during feeding (Siemens 2006). Overall, these infestations facilitate a shift from an aquatic to a more terrestrial invertebrate community, thereby affecting food availability for native fauna foraging in and around lagoons (Siemens 2006). Accordingly, its control and eradication are necessary.in order to maintain the status of the Galápagos Islands lagoons as a Ramsar Internationally Important Wetland (Siemens 2006).

In South Africa, H§fliger & Scholz (1980) documented similar negative affects to native community functions, including competition for space, light, water, and nutrients, replacement of native vegetation, obstruction of water flow, and contaminant seed loading. Further, the invasion of *P. vaginatum* and other nonnative grasses has rendered the sand and mudflats of the Wilderness Lakes Wetland (designated a Ramsar site) unsuitable for wading birds (Randall & Russell 1995).

Paspalum vaginatum is also invasive and has been classified as a "significant environmental weed" in Australia (Randall 2007). It is also invasive in the Hawaiian Islands and the Marshall Islands (Wagner et al. 1999; Whistler & Steele 1999; Vander Velde 2003). Accordingly, PIER (2007) has ranked *P. vaginatum* as a "high risk" invasive species.

SIGNIFICANCE IN SOUTHERN CALIFORNIA

Introduction, Dispersal, and Naturalization.—These naturalized populations represent the first documented records of *P. vaginatum* for California (Webster 1993; Allen & Hall 2003; USDA 2007). *Paspalum vaginatum* has also not been included in major publications on nonnative species established in California (Bossard et al. 2000; Hrusa et al. 2002; DiTomaso & Healy 2003; Bossard & Randall 2007; DiTomaso & Healy 2007; Grewell et al. 2007). Thus far, *P. vaginatum* has not been of concern in southern California (Roberts 1998; Roberts et al. 2004; Rebman & Simpson 2006; Clarke et al. 2007; Riefner & Boyd 2007).

Biologists often have difficulty tracing the source of nonnative organisms and verifying their accidental versus intentional human transport across natural boundaries. However, the arrival of *P. vaginatum* in California is most likely the result of purposeful introductions, presumably for soil stabilization and habitat enhancement projects or more likely for cultivation of turf grass for lawns, parks, and golf courses. Native in the southeastern United States, *P. vaginatum* has been used for restoration of coastal wetlands, stabilization of dunes, banks, and dredge materials in the Gulf States (Duncan & Carrow 1999; NRCS 1999; Fontenot 2007). Accordingly, it may have been introduced for enhancement or restoration of salt marsh habitats in southern California, but we have not been able to confirm this.

However, *P. vaginatum* was introduced to southern California for cultivation as a turf grass during the 1970s and 1980s for research at the University of California South Coast Field Station in El Toro, Orange County, and for commercial production in Indio, Riverside County. It was also planted for turf grass in Laguna Niguel, Orange County, and at Rancho Santa Fe, San Diego County (Henry et al. 1979; Duncan & Carrow 1999). As documented by herbarium records (*Sanders et al. 15885*, RSA; originally identified as *P. distichum*), the earliest escaped and naturalized plants were collected in 1994 near the Salton Sea, Riverside County (Fig. 1). The senior author also made observations of *P. vaginatum* in 1994 (originally identified as *P. distichum* and not collected) at Doheny State Beach, City of Dana Point, Orange County, during surveys conducted for California State Parks (Fig. 1). Species beginning to escape cultivation receive little attention, largely because of the difficulty in identifying and locating them before they become established in native communities. Time lags in plant invasions, a phase when plants are difficult to document during early dispersal, then exponential growth, naturalization in native communities, and subsequent spread describes a typical invasion scenario (Sakai et al. 2001; Schierenbeck et al. 2007). In the case of *P. vaginatum*, plants escaping cultivation from sites in El Toro and Laguna Niguel, Orange County, to native habitats on the coast at Dana Point, Orange County, and from inland sites at Indio to near the Salton Sea in Riverside County, perhaps during the 1990s, appears to be a logical scenario for southern California (Fig. 1).

For this reason, we believe turf plantings may be the most likely source of propagules that dispersed from irrigated urban landscapes downstream to native plant wetland communities. Although its reproduction outside of cultivation and dispersal mechanisms are not well understood, *P. vaginatum* may have been spread vegetatively by animals, carried by mechanized landscape equipment to new sites, or rhizome and stolon fragments may have been dispersed by water during storm events from turf plantings in the uplands into urban drainages and then downstream to native wetland communities.

Paspalum vaginatum is now widely naturalized in southern California's coastal wetlands and at inland habitats near the Salton Sea (Fig. 1). It is most common in estuarine wetlands where it can form monocultures on mudflats, tidal marshes, and shores of estuary lagoons (Fig. 2), or along tidal creeks and sloughs (Fig. 3). Bare soils of tidal mudflats (Fig. 4) and wet sand of disturbed streambeds (Fig. 5) appear to be highly vulnerable to colonization. *Paspalum vaginatum* also grows in many non-saline wetland habitats, including disturbed riparian scrub and slow-moving waters of urban creeks in coastal and desert regions. However, *P. vaginatum* is unlikely to form extensive monocultures or survive long-term competition from large, fast-growing plants and shrubs outside of saline environments.

Urbanization and Wetland Sinks.—*Paspalum vaginatum* is one of many subtropical and tropical non-native plants now established and spreading in southern California. Expanding urbanization has fragmented natural habitats, encouraging nonnative plants cultivated in cities to move easily from human-maintained landscapes to native communities (Vitousek et al. 1996; Cronk & Fennessy 2001). In urban environments, wetlands often accumulate debris and sediments, and receive floodwaters that supply resources (nutrient enrichment, elevated levels of light following flood scour) that may accelerate the growth of opportunistic nonnative plants and facilitate invasion of sunny gaps in the vegetation (Davis et al. 2000; Zedler & Kercher 2004). In addition, hydrological and hydrogeomorphic alterations, accelerated erosion, and other anthropogenic disturbances to wetland and riparian habitats have created numerous opportunities for invasion by nonnative hydrophytes (Newman et al. 1996; Tickner at al. 2001; Werner & Zedler 2002).

Historically, summer drought and the seasonal nature of stream flows in coastal southern California have acted as a barrier to colonization by nonnative facultative wetland plants in the wildland-urban interface (Brigham 2007; Riefner & Boyd 2007). Increased moisture availability in urban environments, and a shift from ephemeral to perennial stream flows owing to waste water discharge into natural drainages in an otherwise summer-dry climate have facilitated the dispersal of these species throughout urbanized southern California (Greer & Stow 2003; Riefner & Boyd 2007).

Biological Traits Promoting Invasiveness in Estuarine Wetlands.—Many wetland plant invasions can be explained by the ecological requirements and attributes of the potentially invasive plant species and the local environmental opportunities afforded by anthropogenic disturbances (flooding, nutrients, propagules, sediments) that may promote invasion and the formation of monocultures in wetland sinks (Werner & Zedler 2002; Kercher & Zedler 2004; Zedler & Kercher 2004). In addition, the selection and breeding for horticultural or agronomic purposes of an individual species, its cultivation in seemingly naïve environments, followed by escape and naturalization, often with detrimental effects to sensitive ecosystems, describes a scenario typical of many invasive plants introduced and now established in the United States (Reichard & White 2001).

Paspalum vaginatum cultivars with improved salt-tolerant characteristics have been developed and are now used widely in the turf grass industry (Lee et al. 2004a,b; Duncan & Carrow 1999; Duncan 2003). *Paspalum vaginatum* is one of the most saline-tolerant turf species available, with ecotypes exhibiting high-vigor root and shoot growth at high salinity levels (Carrow & Duncan 1998; Beard 2002; Lee et al. 2005). Additionally, cultivars have also been developed and evaluated for improved growth rate and transplant survival for restoration and soil stabilization of brackish shorelines, dunes, mudflats, and dredge materials in the Gulf Coast region of the southern United States (Duncan & Carrow 1999; NRCS 1999; Fontenot 2007).

Fig. 2. *Paspalum vaginatum* is often highly invasive in estuarine wetlands and may form monocultures in tidal marshes, on mudflats, and along shores of estuary lagoons. Photograph taken at Malibu Lagoon, Los Angeles County.

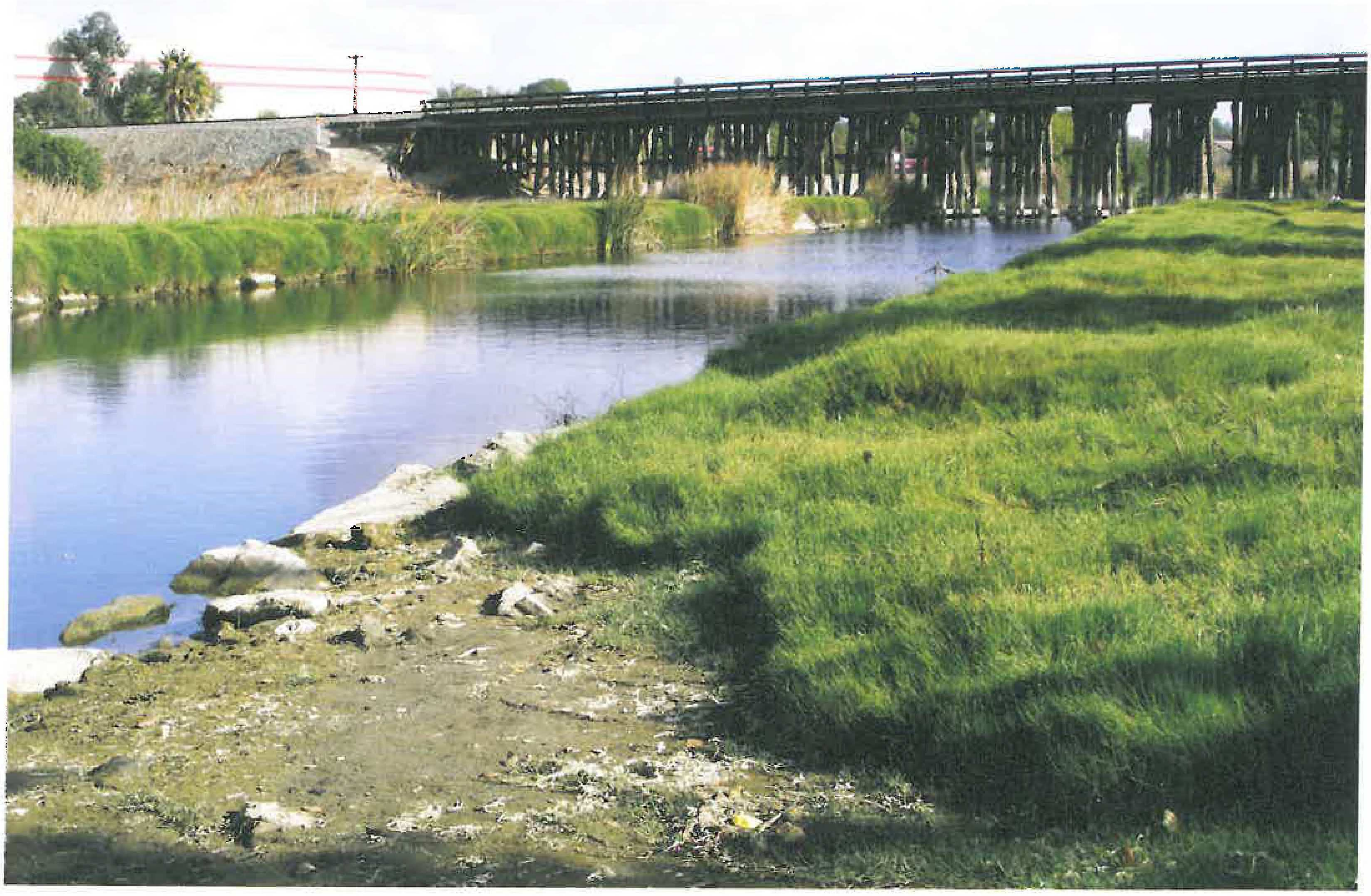

Fig. 3. Marsh habitats and sandy flats along brackish tidal channels and sloughs also support monocultures of *P. vaginatum* that displace native hydrophytes. Photograph taken at Loma Alta Slough, Oceanside, San Diego County.

Fig. 4. Mudflats in tidal wetlands are highly vulnerable to invasions by *P. vaginatum*. Photograph taken at San Diego Creek near confluence of Newport Bay, Newport Beach, Orange County.

Fig. 5. Disturbed urban streambeds characterized by heavy sediment deposition are rapidly colonized by *P. vaginatum*. Rhizome and stolon fragments, spreading from upland landscapes to drainages during rainstorms, start new infestations and act as stepping-stones that facilitate the invasive spread downstream to estuarine wetlands. Photograph taken at Loma Alta Creek, Oceanside, San Diego County.

Table 1. Attributes of *P. vaginatum* that promote invasive behavior in urban wetlands and its ability to form monocultures in estuarine wetlands in southern California (based on the literature and personal observations).

Opportunity or Wetland Niche Open to Invasion	Adaptations and Attributes That Promote Invasiveness and the Formation of Monocultures
Unvegetated mudflats	Inundation tolerance, aggressive colonization, lack of competition from native hydrophytes
Waterlogged and anoxic soils	Aerenchyma in roots
Alterations to hydroperiod, fluctuating water depth, and shallow water	Broad ecological tolerance, rhizomes and stolons that float and grow out into water, adventitious roots, and rapid growth
Saline soils	High salt tolerance, sustained vigor and shoot growth in salt-affected sites
Flooding, nutrient influx, and sediment deposition	Rhizome and stolon fragments dispersed by water, aggressive colonization and establishment, dense persistent rhizome mats, and lack of competition from native hydrophytes
Summer-wet urban drainages	Warm-season growth with C_4 pathway, wide pH tolerance and adaptation to diverse soil types
Canopy gaps	High light requirements, aggressive colonization, and lack of competition from fast-growing native hydrophytes

Accordingly, *P. vaginatum* cultivars could become invasive, and might have significant detrimental effects to native estuarine ecosystems if they escape from urban environments or if they are used in restorations outside the native range of the species, including the southwestern United States. The biological adaptations and attributes of *P. vaginatum* that promote its invasive behavior associated with anthropogenic disturbance in urban wetlands, and its ability to form monocultures in native estuarine wetlands are summarized in Table 1.

Impacts to the Environment.—Our field observations indicate *P. vaginatum* is a threat to the ecological function of estuarine wetlands in southern California. We currently lack experimental data to substantiate the changes to wetland composition and structure that we have observed. However, strong anecdotal evidence and quantitative data gathered in other countries provide sufficient baseline information indicating its impacts to native ecosystems may be significant and comparable to the well-documented invasions by introduced *Spartina* species (Graeme & Kendal 2001; Shaw & Allen 2003; Dana et al. 2004; Siemens 2006).

Invasions of *Spartina* species, especially *S. alterniflora* and its hybrids, have engineered the alteration of habitats critical to endangered species, conversion of tidal mudflats to meadow, changes to creek morphology and hydrological regimes, failure of local wetland restoration projects, and local extinctions of the native California cord grass (*Spartina foliosa* Trin.) in the San Francisco Estuary (Ayres et al. 2004; Callaway 2005; Strong & Ayres 2005; California Conservancy 2007; Grewell et al. 2007). Comparisons of the environmental impacts of introduced *Spartina* species versus *P. vaginatum* are summarized in Table 2.

DISCUSSION

Wetlands are uniquely important natural resources that are highly vulnerable and threatened in southern California (Ferren & Fiedler 1993). Poor historical documentation, rapidly expanding urbanization, habitat fragmentation, and poorly coordinated conservation programs have resulted in the long-term, unmitigated loss and degradation of wetland resources, which are proportionally higher in California than in other parts of the United States (Dahl 1990; Grewell et al. 2007). To compound historic losses, wetland invasions by nonnative species also threaten native biodiversity and ecosystem function, which may soon surpass habitat loss as the main cause of environmental degradation (Chapin et al. 2000; Grewell et al. 2007).

TABLE 2. Comparison of impacts to estuarine wetland composition and structure documented for introduced *Spartina* species in the San Francisco Estuary, northern California, versus observed or potential impacts of *P. vaginatum* in southern California's estuarine wetlands.

Impacts of ***Spartina*** Species: San Francisco Estuary	Impacts of ***Paspalum vaginatum***: Southern California Estuarine Wetlands
Impacts to sensitive species: competes for space with the federally listed *Cordylanthus mollis* subsp. *mollis*	**Impacts to sensitive species:** competes for space with the federally and state-listed *Cordylanthus maritimus* subsp. *maritimus*
chokes channels used by the endangered California clapper rail to forage, and displaces pickle weed marsh of the endangered salt marsh harvest mouse	insufficient information available for potential impacts to listed animal species potentially competes with, grows over, or inhibits germination of other sensitive plants: *Eleocharis parvula*, *Lasthenia glabrata* subsp. *coulteri*, and *Suaeda esteroa*
Converts tidal mudflats to meadow or marsh: coalesces to form cord grass meadows	**Converts tidal mudflats or sand flats to meadow or marsh: dense mats exclude or smother low-stature halophytes**
accretes and stabilizes sediment among dense shoots, which increases the elevation of the mud flat for further colonization	stabilizes and possibly accretes sediment and organic detritus among dense shoots, to stolons, and rhizomes for further colonization
	high shoot, rhizome, and stolon density potentially excludes or could alter composition of burrowing fauna
Loss of shorebird foraging habitat: fills in the open mud of channels and sloughs, altering marsh hydrology	**Loss of shorebird foraging habitat:** colonizes mudflats, tidal creek channels, and shallow lagoon waters, which could become unsuitable for wading birds
Loss of critical channel habitat: alters marsh hydrology and channel habitat	**Loss of critical channel habitat:** insufficient information available
Local extinction of the native California cord grass (*S. foliosa*): conversion of native California cord grass marsh to dense swards of *S. alterniflora* hybrids	**Local exclusion of native halophytes:** grows over and smothers low-stature species of *Atriplex*, *Batis*, *Cressa*, *Distichlis*, *Frankenia*, *Isolepis*, *Jaumea*, *Limonium*, *Monanthochloe*, *Salicornia*, *Spergularia*, and *Triglochin*
Failure of wetland restoration project objectives: displaces and excludes recruitment of native species	**Failure of wetland restoration project objectives:** potentially displaces and excludes recruitment of native species

Paspalum vaginatum is a highly aggressive invasive species that poses a serious threat to wetland diversity by transforming the physical structure and biological composition of tidal marshes and mudflats in southern California. Because the use of *P. vaginatum* will probably increase in turf grass landscapes across urbanizing southern California, it is unlikely that the species will decline. In fact, *P. vaginatum* will most likely spread to new regions, which points to an immediate need to control or eradicate expanding infestations.

Management and research programs have been developed to monitor and restore *P. vaginatum*-affected wetlands in other countries (Graeme & Kendal 2001). Potential strategies and resource management topics relevant for urbanized southern California are:

1) Create awareness and educate biologists, field researchers, and resource agencies regarding the invasive behavior of *P. vaginatum*;

2) Add *P. vaginatum* to the California Invasive Plant Council list of plants of greatest ecological concern (severe ecological impacts on physical processes, plant and animal communities, and vegetation structure);
3) Expand field surveys to determine the complete distribution and abundance in native habitats, quantify expanding use in urban landscapes, and determine if it is used in restorations;
4) Assign *P. vaginatum* an obligate wetland indicator status (OBL, found >99% of the time in wetlands) for California (Region 0) on the National List of Plant Species that Occur in Wetlands to aid wetland delineations;
5) Identify and monitor adverse ecological changes to wetland ecosystems and potential impacts to sensitive floral and faunal elements;
6) Develop habitat- and region-specific control programs;
7) Conduct ecological risk assessments of potential control techniques to avoid secondary impacts to sensitive resources.

The introduction and naturalization of *P. vaginatum* demonstrates the urgent need to implement detailed floristic monitoring of wetland communities in southern California's rapidly urbanizing communities. Early detection of new invasive plants would likely minimize their impacts on biodiversity and ecosystem functions, and reduce the high cost of control and eradication. Declines in biodiversity of wetland ecosystems in urbanized environments are becoming a major concern to resource managers, especially in California, which has the highest number of wildland-urban interface housing units (and associated parks, lawns, recreational landscapes planted with turf grass) in the United States (McKinney 2002; Radeloff et al. 2005; Schwartz et al. 2006). Accordingly, the widespread utility of *P. vaginatum* for turf landscapes, and potential use in wetland restorations, may require the participation of agronomists, biologists, conservation groups, and local and federal government resource agencies where wetland biodiversity and conservation objectives potentially conflict with urban landscape management practices in southern California.

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